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A COMPARATIVE MORPHOLOGICAL STUDY  
OF THE PROVENTRICULUS OF ANTS  
(HYMENOPTERA : FORMICIDAE)

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WITH TWENTY-FIVE PLATES

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No. 8 — *A Comparative Morphological Study of the  
Proventriculus of Ants (Hymenoptera:  
Formicidae)*

By THOMAS EISNER<sup>1</sup>

CONTENTS

INTRODUCTION .....	441
ACKNOWLEDGMENTS .....	445
PART I: MATERIALS AND METHODS .....	445
Cuticular framework preparations (p. 446); histological serial sections (p. 447); method of illustration (p. 448).	
PART II: TYPES OF FORMICID PROVENTRICULI .....	449
MYRMECIOID COMPLEX .....	449
Subfamily Myrmecinae .....	449
<i>Myrmecia</i> (p. 449, fig. 4)	
Subfamily Pseudomyrmecinae .....	452
<i>Pseudomyrmex</i> (p. 452, fig. 5)	
Subfamily Aneuretinae .....	453
<i>Aneurtus</i> (p. 453, fig. 6)	
Subfamily Dolichoderinae .....	453
<i>Hypoclinea</i> (p. 453, fig. 7); <i>Leptomyrme</i> x (p. 454, fig. 9); <i>Liometopum</i> (p. 455, fig. 8); <i>Tapinoma</i> (p. 456, fig. 26); <i>Az-</i> <i>teca</i> (p. 458, fig. 30); <i>Iridomyrmex</i> (p. 459, fig. 32); <i>Frog-</i> <i>gattella</i> (p. 460); <i>Turneria</i> (p. 461); <i>Dorymyrmex</i> (p. 461, fig. 42); <i>Forelius</i> (p. 462, fig. 40); <i>Conomyrma</i> (p. 463, fig. 33); <i>Technomyrmex</i> (p. 464, fig. 48).	
Subfamily Formicinae .....	465
Asepalous formicine proventriculus .....	465
<i>Notoncus</i> (p. 465, fig. 50); <i>Melophorus</i> (p. 469, fig. 52); <i>Aeropyga</i> (p. 469, fig. 51); <i>Anoplolepis</i> (p. 469, fig. 64); <i>Acantholepis</i> (p. 469, fig. 65); <i>Diodontolepis</i> (p. 469); <i>Myrmoterax</i> (p. 469, fig. 66).	
Sepalous formicine proventriculus .....	470
<i>Camponotus</i> (p. 470, fig. 68); <i>Formica</i> (p. 473, fig. 69); <i>Notostigma</i> (fig. 76); <i>Lasius</i> (fig. 78); <i>Prenolepis</i> (fig. 77); <i>Myrmecocystus</i> (p. 474, fig. 79); <i>Gesomyrmex</i> (fig. 80); <i>Paratrechina</i> (fig. 81); <i>Cataglyphis</i> (fig. 82); <i>Brachymyrme</i> x	

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(fig. 84); <i>Oecophylla</i> (fig. 83); <i>Gigantiops</i> (p. 474); <i>Dendromyrmex</i> (p. 474); <i>Opisthopsis</i> (p. 474); <i>Polyergus</i> (p. 474); <i>Polyrachis</i> (p. 474); <i>Pseudolasius</i> (p. 474).	
Proventriculi with incipient sepals .....	474
<i>Cladomyrma</i> (p. 474, fig. 85); <i>Myrmecorhynchus</i> (p. 474, fig. 86).	
PONEROID COMPLEX .....	475
Subfamily Ponerinae .....	475
<i>Odontomachus</i> (p. 475, fig. 90); <i>Amblyopone</i> (p. 476, fig. 91).	
Subfamily Cerapachyinae .....	476
<i>Phyragaces</i> (p. 476, fig. 92).	
Subfamily Myrmicinae .....	477
<i>Pogonomyrmex</i> (p. 477, fig. 95); <i>Hylomyrma</i> (p. 478).	
Subfamily Dorylinae .....	478
<i>Eciton</i> (p. 478, fig. 93).	
THE STOMODAEAL VALVE .....	478
IDENTITY OF THE SEKRETSCHICHT OF EMERY (1888) ..	479
PART III: DISCUSSION .....	481
LITERATURE CITED .....	487
KEY TO ABBREVIATIONS .....	489

## INTRODUCTION

Adult Hymenoptera are distinctly discontinuous in their feeding habits, and subsist very largely on fluids (Bischoff '27). The relatively large amount of liquid nutrient gathered during one of the intensive feeding periods is not passed directly into the midgut (text fig. 1, *m. g.*), but is first temporarily retained within a sac-like dilation of the stomodaeum called the crop (text fig. 1, *cr.*). At intervals, controlled amounts of liquid are released from the crop to the midgut. Since in this way food is passed gradually into the midgut, thereby avoiding a sudden dilution of midgut enzymes at feeding, the digestive and absorptive processes within the midgut proceed at optimal efficiency. The organ that regulates the delivery of fluid from crop to midgut is the proventriculus (text fig. 1, *pv.*). In adult Hymenoptera the proventriculus, as usually developed, is no mere strait between crop and midgut. It consists of a relatively voluminous, strongly-muscled, bulb (text figs. 2, 3), opening anteriorly to the crop through a cruciform portal, and posteriorly into the midgut through a slender, tubular, stomodaeal valve.

From the structure of the organ it is clear that this type of proventriculus represents a distinct adaptation to the fluid nature of the diet. It is, in fact, nothing but a pump, with intake and exhaust valves provided respectively by the portal and the stomodaeal valve. Proventricular activity consists of rhythmic contractions and expansions of the bulb by means of which a regulated pumping is accomplished (Bailey '52, Schreiner '52). Small particulate matter, such as pollen grains, present no obstacle to proventricular pumping. We know, for instance, that in *Prosopis*, *Vespa*, and *Bombus*, even relatively dense suspensions of pollen grains are effectively transferred to the midgut without proventricular obstruction (Bailey '54). In *Apis*, the proventriculus may even, under special circumstances, convey pollen grains to the midgut independently from their liquid medium (Bailey '52, Schreiner '52); but this filtering ability

is probably secondary to the primary fluid-pumping function of the organ (Bailey '54).

Among the hymenopterous insects thus far investigated, the proventriculus is monotonously uniform in structure from family to family. This circumstance throws into striking relief the exceptional group: the ants. Within this single medium-sized family, the proventriculus shows a greater diversity of structural types than can be found in any other insect family—greater even than in most entire orders.

According to the theory of Wheeler ('23), a fundamental bond of social life among the ants is the exchange of nutrient through regurgitative feeding. In adaptation to regurgitative feeding the crop assumes a new and overwhelmingly important function in the social community. It serves not only as a receptacle for the nutrient reserves of the individual, but also as a communal reservoir, or, as Forel aptly termed it, a "social stomach," from which the non-foraging members of the community may derive their nourishment. Some of the higher ants, in which regurgitative feeding achieves its highest degree of specialization, have even developed special storage castes ("repletes") with enormously distended crops and expansible gasters (e.g. *Leptomyrmer*, *Melophorus*, *Prenolepis*, *Myrmecocystus*, *Proformica*, etc.).

In ants, as in all Hymenoptera, the proventriculus serves primarily as a pump. However, the development of a crop capable of storing nutrient, not only *in amounts far beyond those required by the individual forager*, but also for *prolonged periods of time*, has been accompanied by modifications in the proventriculus allowing that organ to assume the additional function of effectively damming the posterior outlet of the crop. The ant proventriculus is thus seen to serve a dual purpose, being responsible not only to the individual, for whom it regulates the nutrient supply to the midgut, but also to the community, which it serves by acting as a passive dam to the "social stomach." During evolutionary refinement of its emergent social function as

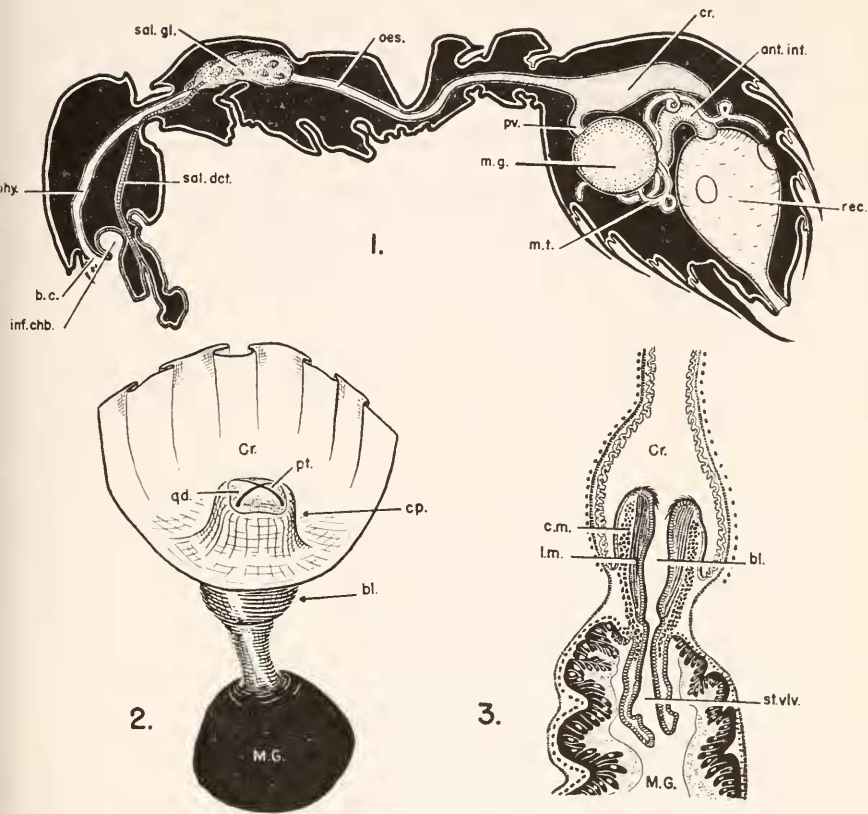


Fig. 1. Digestive tract of the ant *Myrmica rubra* (simplified, with some cephalic structures omitted; after Janet). Abbreviations: *ant. int.*, anterior intestine; *b. c.*, buccal cavity; *cr.*, erop; *inf. chb.*, infrabuccal chamber; *m. g.*, midgut; *m. t.*, malpighian tubule; *oes.*, oesophagus; *phy.*, pharynx; *pv.*, proventriculus; *rec.*, rectum; *sal. dct.*, salivary duct; *sal. gl.*, salivary gland.

Fig. 2. Proventriculus of *Apis* (after Snodgrass, relabelled). Abbreviations: *bl.*, bulb; *cp.*, cupola; *Cr.*, crop; *M. G.*, midgut; *pt.*, portal; *qd.*, quadrant.

Fig. 3. Longitudinal section through proventriculus of *Apis* (after Snodgrass, relabelled). Abbreviations: *c. m.*, circular muscles; *l. m.*, longitudinal muscles; *st. vlv.*, stomodaeal valve; other labels as in Figure 2.

a dam, the ant proventriculus has solved its new mechanical problems by means of a number of different morphological changes, accounting for the extraordinary diversity in structure by which the organ has come to express itself in the ants.

*The present study has as its chief objectives the analysis of structure, and the explanation of function, of each of the principal kinds of proventriculi known to occur among the ants. This structural analysis draws from, and is resynthesized with a view to augmenting, the general body of knowledge concerning formicid evolution. All three elements of this approach — anatomical, mechanical, and phylogenetic — have been inextricably involved in each step of the study.*

The ant proventriculus has been the subject of considerable interest in the past; yet, despite several involved descriptions of its anatomy that have appeared, its exact function and mode of action have never been properly understood. Due to its structural variability, the organ has been used extensively as a taxonomic character in the classification of the Dolichoderinae and Formicinae, and in phylogenetic speculations concerning these and other groups. The first accurate anatomical study of the dolichoderine-formicine proventriculus was that of Forel (1878). Emery (1888) followed up Forel's work in a classic comparative monograph, still the basic reference on this organ. He reviewed most of the dolichoderine and formicine tribes, as well as the aberrant myrmicine tribe Cephalotini. Additional concise descriptions of the proventriculus of the Dolichoderinae and Formicinae were given in 1912 and 1925 in the fascicles of Wytsman's *Genera Insectorum* dealing with these groups. The most recent work deals only with the aneuretine proventriculus (Wilson, Eisner et al. '56) and with the specialized camponotine type (Eisner and Wilson '52). Wherever necessary, reference is made to these works throughout this paper.

The suprageneric classification of the family Formicidae followed here is that advanced by Brown ('54). The aneuretines are given subfamilial rank in accordance with Wilson, Eisner et al. ('56). On the advice of W. L. Brown, Jr. and E. O. Wilson, I am avoiding the use of tribal designations, classification at this level being artificial and currently under revision.



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I also wish to thank Dr. E. O. Wilson for supplying some of the formicine genera, for help in field work, and for offering advice during the earlier phases of the study. The section devoted to the sepalous formicine proventriculus represents the results of a study conducted jointly with Wilson in 1952, and recently published (Eisner and Wilson '52). The contents of this paper have been incorporated herein in slightly modified form.

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## PART I

## MATERIALS AND METHODS

It is impossible fully to understand any proventriculus without considering the closely interdependent structure and function of the two major organic constituents, the cuticular framework and the muscular envelope. Structural data were obtained principally from two types of microscopic preparations. The first of these consisted of the isolated proventricular framework divested of all attached cellular portions. The second type of

preparation consisted of the simple serial sections of the whole proventriculus. The functional and phylogenetic considerations were derived from a careful comparative study of these preparations and such other incidental data as became available.

The following is a brief outline of the procedure used in the making of the preparations and a brief account of the method of illustration employed, with a consideration of its limitations.

#### Cuticular framework preparations

This method is outlined here in some detail, since it may be of aid to the systematist who uses the ant proventriculus as a taxonomic character.

In order to remove all cellular constituents from the proventriculus, the whole ant is immersed in hot (*ca.* 90°C) 10% aqueous KOH for  $\frac{1}{2}$  to 1 hour, or in the same solution at room temperature for 8 to 15 hours. Specimens from either fluid preservative or dry mounts may be treated in this way.

The whole ant is then transferred through several changes of distilled water to remove the alkali, and finally to 70% alcohol, where the proventriculus is dissected out. To this end, a small window is first cut in the gaster, through which the crop can readily be seen as a thin cuticular sac extending backwards from the petiole; the proventriculus itself appears as a small terminal protuberance on the crop. At no time should the proventriculus be severed from the crop, since the crop provides an ideal hold-fast by which the proventriculus may be transferred through the various solutions which follow. Furthermore, the positional relationship and proportions of the two organs are in themselves important things for the observer to note. The crop with the proventriculus is seized with fine forceps, extracted from the gaster and transferred directly into the stain.

Chlorazol black E (1% in 70% alcohol) proved to be the most suitable of the stains used (Pantin '48). One to five minutes suffices for adequate staining; overstained specimens are usually, but not always, readily destained in 70% alcohol.

Other cuticular stains such as eosin, acid fuchsin, fast green and picro-cresote (Kennedy '49) offered no advantages over chlorazol black E. Acid fuchsin occasionally proved useful as a counterstain to chlorazol black; the latter stain has a low affinity

for the cupolar or sepalar region of the proventriculus, while acid fuchsin has a strong affinity for these regions only, and was therefore especially useful where it was otherwise impossible to delimit the exact extent of the portal opening of the proventriculus.

The specimen is then passed through two changes of 100% alcohol for about 3 minutes each, and into cedar oil, where it may be stored indefinitely. If whole mounts are desirable, the cedar oil is rinsed off with xylol, and the specimen mounted under a coverslip in balsam or synthetic resin.

In cases in which valuable dried specimens, such as holotypes or uniques, must be studied, the proventriculus can usually be removed without materially damaging the ant. To isolate the proventriculus from such a sample, the specimen is first relaxed in a suitable fluid, such as Barber's fluid or a mild detergent-water mixture, and then the crop and proventriculus are extracted together through an incision in the membrane between the first and second gastric segments. The location of the incision may, of course, vary with the kind and condition of the ant, but a careful and commonsense approach adapted to the individual specimen will usually yield a good proventriculus. As Forel long ago noted, this operation can be performed so neatly that the re-mounted ant is only the better for its incidental bath. Once isolated, the crop and proventriculus can be treated with cold 10% KOH until free of soft tissues, and then handled like any other proventriculus.

#### Histological serial sections

Unfortunately, many of the genera available for this study were either dried, or had been stored in alcohol for many years, which rendered them useless for histological study. There was also available, however, an adequate series of representative genera properly preserved by histological fixatives (Schaudinn's, Bouin's, Carnoy's). Some of the material that had been preserved in alcohol for relatively short periods of time (about 5 years or less) yielded adequate and, in fact, often remarkably good histological preparations.

Serial sections were made by routine histological technique. The proventriculi were embedded in *Tissuemat* ( $\frac{1}{2}$  hour), sec-

tioned at 5 to 10 micra, and stained with Ehrlich's hematoxylin and eosin, or in some cases with Masson's trichrome, Mallory's triple or Heidenhain's iron-hematoxylin. Both longitudinal and transverse sections were always made.

### Method of Illustration

The drawings of ant proventriculi used throughout this paper are of two distinct types.

The first of these consists of three-dimensional semi-diagrams of the whole cuticular framework of the proventriculus. The camera lucida drawings on which these illustrations are based were made as follows. With the proventriculus submerged in cedar oil in a small dish placed under the dissecting microscope, the fine, drawn-out end of a glass capillary needle was introduced into the proventriculus through the point of intersection of the slit-like anterior openings (portal) of the organ. The opposite end of the needle was held in a universal joint by means of which the glass needle could be turned and the proventriculus oriented in the desired way. The hollow glass needle draws in the oil by capillarity, and in so doing becomes almost transparent and does not hide any of the structural details of the proventriculus. Camera lucida drawings were made with 15x ocular and 6x objective. The histological serial sections were of aid in filling in some of the more inconspicuous structural detail, not seen through the dissecting microscope.

In some of those few proventriculi studied in which the cuticular framework is excessively thin and flaccid, usually losing its shape in the absence of the supporting musculature (the ponerine, cerapachyine, doryline, and myrmicine representatives, and to some extent also the aneuretines and pseudomyrmecines), the drawings are in large part reconstructions based on the serial sections, and are labelled as diagrams.

With the exception of the conspicuous rugae on the outer margins of the plicae of the bulb, no effort was made in any of these drawings to represent the finer details of cuticular sculpturing. Wherever possible, these details were represented in the histological drawings discussed below.

For the purpose of clarifying some of the internal intricacies of the proventriculi, the cuticular framework is occasionally

represented with certain sections cut away. The depiction of the cutaways was based on the serial sections.

The second type of illustration consists of semi-diagrams of selected histological cross sections and longitudinal sections through the proventriculus, and were made with the aid of a camera lucida.

Due to the variety of fixatives used, the material served only for gross histological study, and lacked the uniformity necessary for comparative cytological observations of any value. The illustrations are therefore semi-diagrammatic, inasmuch as no attempt was made to represent intracellular detail. In a limited number of cases the only histological sections obtained were oblique, rather than transverse or longitudinal, and the drawings represent reconstructions from camera lucida outlines of the oblique sections. Wherever such reconstruction was employed, the drawings are labelled as *diagrams*.

The outstanding difficulty encountered in the interpretation of the histological sections was raised by the outermost longitudinal muscle fibers of the proventriculus (*l.m. 3* or similarly disposed fibers). These fibers usually consist of only a few scattered strands, which during histological processing may shrink away from their insertions on the cuticle, thereby becoming easily displaced, especially since they often lack the support of other tissues and lie free in the hemocoel. Tracing such muscle fibers through successive sections was difficult at best and sometimes impossible.

## PART II

### TYPES OF FORMICID PROVENTRICULI

#### MYRMECIOID COMPLEX

##### Subfamily MYRMECIINAE

#### MYRMECIA Fabricius

*Species examined:* *M. regularis*\* Crawley, *M. piliventris* F. Smith, *M. nigrocincta* F. Smith, *M. vindex*\* F. Smith, *M. forficata*\* (Fabricius).

\* An asterisk is used herein to denote those proventriculi which were sectioned histologically. A lack of an asterisk indicates that only cuticular framework preparations were made.

The proventriculus of *Myrmecia* is one of the least specialized among that of ants, and in most major respects it is similar to that of the few other aculeate hymenopterous families in which the organ has been described.

The cuticular framework (Fig. 4) consists of a thin-walled, flask-shaped *bulb* (*bl.*), opening anteriorly through a wide, roughly cruciform *portal* (*pt.*). The walls of the bulb are four broad, sclerotized, inwardly-curved plates, joined basally and merging into the slender, tubular *stomodaeal valve* (*st. vlv.*). The plates are separated one from another by relatively narrow longitudinal strips of thin, flexible cuticle, the *pleats* or *plicae* (*pl.*). The plates themselves are here termed *interplicaries* (*interpl.*). The interplicaries extend free beyond the plicae and the portal to project into the lumen of the crop as four apically rounded lobes or *quadrants* (*qd.*), collectively constituting the *cupola* (*cp.*). Actually, the cruciform shape of the portal is determined by the presence of the cupolar quadrants. The inner sclerotized surface of the quadrants is covered with relatively sparse short pile (Figs. 10, 12).

The bulb is surrounded by a strongly developed layer of circular muscles (Figs. 10, 13, 14; *c.m.*). With the exception of the innermost fibers, which insert on the lateral margins of the plicae, the circular muscles envelop the bulb without attachment to the cuticle.

The longitudinal muscles are arranged in three distinct groups (Figs. 10, 12, 13, 14; *l.m.1*, *l.m.2*, *l.m.3*). The most strongly developed of these (*l.m.1*) extends over the interplicatory cuticle of the bulb, originating posteriorly near the base of the bulb and inserting anteriorly on the quadrants of the cupola. A second group (*l.m.2*) inserts along the posterior half of the interplicatory plates, pierces the circular muscles, and fans out to become a part of the longitudinal musculature of the midgut. The third group (*l.m.3*) consists of only a few scattered fibers that insert on the quadrants, and extend posteriorly over the circular muscles to become continuous with *l.m.2*.

It proved impossible to determine the exact fate of those longitudinal muscles that approach the bulb from the crop, although the preparations suggested that these fibers distribute themselves among the various intrinsic muscles of the proventriculus (see dotted lines, Fig. 10).

In the arrangement of its longitudinal muscles, the *Myrmecia* proventriculus is unique: all other ant proventriculi examined, with the possible exception of *Pseudomyrmex*, *Aneuretus* (see next below) and some genera of the Poneroid complex, lack the *l.m.2* fibers.

A longitudinal section through the stomodaeal valve and associated structures (Fig. 11) shows how the extremely thin and flexible cuticular intima of the valve extends far into the lumen of the midgut and then turns inside out and back upon itself so as to form a compound tube. A strong muscular sphincter embraces the valve at the point of emergence from the bulb. Figure 11 is of interest also in that it shows in histological detail the nature of the foregut-midgut junction. Attention is called to the conspicuous columnar cells (*a*) grouped as a ring around the stomodaeal valve at the point where the latter perforates the midgut. The nature of these cells becomes clear from the work of Dobrovsky ('51) who has shown that in *Apis* these cells form a continuous barrier that separates the foregut from the midgut during the course of prepupal reorganization. At this time the developing stomodaeal valve is held back as an invagination within the bulb, and it is not until later that the cellular barrier is pierced by the intrusion of the valve into the midgut. A point of incidental interest is that the *basement membrane* (*b.m.*), which is strongly eosinophilic and readily traced, forms a continuous sheet over the foregut and midgut epithelium.

In all other ant proventriculi, the stomodaeal valve is essentially similar to that of *Myrmecia*, and except for some minor (but functionally significant) variation in the degree of development of the muscular sphincter (see page 478), no further consideration will be given to the stomodaeal valve in subsequent proventriculi.

My interpretation of the function of the *Myrmecia* proventriculus is as follows. The circular and longitudinal muscles act as antagonists to one another in compressing and expanding the bulb. By the combined action of the various longitudinal fibers, the interplenary plates of the bulb first spread apart from one another with the unfolding of the plicae, and then are flattened out. The quadrants of the cupola separate, and crop fluid is admitted through the widened portal into the expanded bulb. A forward flow of liquid from the midgut is prevented by the

stomodaeal valve, the thin wall of which collapses under the pressure of the midgut contents. By the contraction of its circular muscles, the bulb is then compressed and its contents forced back through the stomodaeal valve into the midgut. Backflow to the crop is hindered by the tight closure of the cruciform portal (approximation of the quadrants) and by a tight folding of the membranous plicae, closed by the circular fibers along their margins.

In addition to its function as a one-way valve, the stomodaeal valve undoubtedly serves also as a flexible, self-adjusting link, which by bending is capable of adjusting to peristalsis and volume changes of the crop.

The proventriculus of *Myrmecia* apparently is no better adapted to serve as a dam for the crop than is that of other Hymenoptera. It is evident from the structure of the organ that prolonged damming is possible only if either the cruciform portal or the stomodaeal valve is maintained tightly occluded under sustained muscular contraction. In preserved proventriculi of all *Myrmecia* species examined, the portal was always seen to be slightly agape, suggesting that sustained occlusion is maintained exclusively at the level of the stomodaeal valve, which in this genus is provided with a particularly powerful sphincter.

#### Subfamily PSEUDOMYRMECINAE

#### PSEUDOMYRMEX Lund

*Species examined: P. pallidus\** (F. Smith).

In its principal features, the proventriculus of *Pseudomyrmex* (Fig. 5) is similar to that of *Myrmecia*, and it can be safely assumed that it functions in much the same way. In *Pseudomyrmex* the quadrants of the cupola are shaped to fit together more closely at the axis, resulting in a more narrow cruciform portal, and a more compact cupola.

The *Pseudomyrmex* material available was in such a poor state of preservation that exact delineation of the longitudinal musculature was impossible. Although the presence of *l.m.1* and *l.m.3* fibers could be determined with certainty (Figs. 15, 16), there remains some doubt concerning the presence of *l.m.2*. A few fibers, strongly suggestive of *l.m.2* were seen in cross sections to



extend through the circular muscles at the level of the posterior third of the bulb (see *l.m.2* (?), Fig. 16), but final proof of the presence of *l.m.2* must await further investigation.

### Subfamily ANEURETINAE

#### ANEURETUS Emery

*Species examined: A. simoni*\* Emery.

In all of its major features, this proventriculus (Fig. 6), like that of *Pseudomyrmex*, conforms closely to that of *Myrmecia*.

The *l.m.1* and *l.m.3* fibers are fully retained (Fig. 21). Although I found no evidence for the presence of *l.m.2* fibers, I must admit that some uncertainty remains regarding their absence; the small size of the proventriculus, and the rather poor condition of the preparations available, made precise observations difficult.

In view of the overall structural similarity of this proventriculus with that of *Myrmecia* and *Pseudomyrmex*, its function is probably also much the same.

### Subfamily DOLICHODERINAE

#### HYOCLINEA Mayr

*Species examined: H. pustulata*\* (Mayr).

The cuticular framework of the proventriculus of *Hypoclinea* (Fig. 7), although distinctive in its ovoid bulb and flattened dome, still conforms to the basic structural plan of *Myrmecia*, *Pseudomyrmex*, and *Aneuretus*, except that the plicae have become sclerotized toward the base of the bulb.

Histologically, the longitudinal musculature has undergone a simplification by the loss of *l.m.2* (Fig. 17). In *Hypoclinea* this could be ascertained with certainty. Only *l.m.1* and *l.m.3* are retained (Figs. 17-20). As will be recalled, the main function of *l.m.2* in *Myrmecia* is to expand the bulb by pulling outward on the interpleuric plates. With the sclerotized posterior parts of the plicae, the base of the bulb in *Hypoclinea* forms a cup of uninterrupted relatively thick cuticle, capable of elastic expansion by itself when the circular muscles relax. *l.m.2* has therefore become superfluous and is lost. The *l.m.1* and *l.m.3*

fibers serve mainly to disengage the cupolar quadrants so as to open the bulbar portal during the intake phase of proventricular activity, and from their attachment, it can be seen that they play no major part in the expansion of the bulb itself. Except for the fact that bulb expansion has become a passive process, the action of the *Hypoclinea* proventriculus is probably similar to that of *Myrmecia*.

#### LEPTOMYRMEX Mayr

*Species examined:* *L. pallens*\* Emery, *L. cnemidatus* Wheeler.

The proventriculus of *Leptomyrmex* (Fig. 9) has become specialized in several major respects. The cupola is characteristically concave in its anterior aspect. The bulb is relatively small, and occupies less than the posterior half of the proventriculus. In the anterior half, the interpleicary plates are thickened and pinched inward so as to frame a narrow cruciform tract, the *occlusory tract* (*occ. tr.*), an inward extension of the cruciform portal of the cupola. The entire occlusory tract and cupola are lined with dense, long, pile (Figs. 23, 24).

The walls of the occlusory tract are still articulated laterally by thin, flexible plicae, but as the occlusory tract opens posteriorly into the bulb, the plicae lose their membranous character and thicken to become sclerotized and hollow (C-shaped in cross section), reinforcing the bulb at its four angles.

Histologically, *Leptomyrmex* resembles *Hypoclinea* in that *l.m.2* is absent, and only *l.m.1* and *l.m.3* are retained (Figs. 23, 24, 25).

In its pumping action, the proventriculus of *Leptomyrmex* resembles that of *Hypoclinea* inasmuch as the bulb, being laterally reinforced by sclerotized plicae, is so constituted as to expand through its own elasticity. The longitudinal muscles serve only to widen the occlusory tract (the walls of which are allowed to separate by the flexibility of the plicae), thereby opening the pathway by which fluid enters the bulb.

In the acquisition of an occlusory tract we see in *Leptomyrmex* the first major specialization serving to improve the damming potential of the proventriculus. The extensive, relatively narrow, and densely pilose occlusory tract would seem capable by itself of effectively containing to a large extent the posteriorly

directed pressure exerted by the crop contents. Thus, the need for muscular force in the maintenance of proventricular occlusion has become somewhat reduced, and the efficiency of the damming action of the proventriculus correspondingly increased.

### LIOMETOPUM Mayr

*Species examined: L. sp.\* (near apiculatum Mayr).*

Although superficially *Liometopum* (Fig. 8) is quite distinct from *Leptomyrmea*, its general structural plan betrays its debt to a stock common to these two genera. Like *Leptomyrmea* *Liometopum* has an extensive oclusory tract, and the bulb itself is considerably reduced in size. Both the oclusory tract and cupola bear dense, long pile (Fig. 22). In contrast to that of *Leptomyrmea*, the cupola of *Liometopum* is broad and convexly reflexed, and is somewhat more rigid in consistency than any previously discussed. The plicae of *Liometopum* are, as in *Leptomyrmea*, fully sclerotized at the level of the bulb. Unlike in *Leptomyrmea*, the plicae are also somewhat thickened at the level of the oclusory tract, although they undoubtedly still retain sufficient flexibility to be readily unfolded when the oclusory tract is dislodged during bulbar intake. The ready mobility of the oclusory tract is clearly evidenced by prying with a glass needle. The muscles (Fig. 22) are arranged as in *Leptomyrmea*.

In its pumping action, *Liometopum* cannot differ grossly from *Leptomyrmea*. Some improvement might be afforded by the more rigid reflexed cupola, which acts to assure a passively maintained intrusion of the anterior proventriculus into the crop and thereby provides greater freedom of access to the cruciform portal. In the genera discussed previously, superficially similar intrusion of proventriculus into crop is also seen, but in these the texture of the cupola is largely membranous, and its intrusion seems to be maintained entirely by the tension of those longitudinal muscles extending from the crop over the proventriculus.

In its action as a dam, the *Liometopum* proventriculus shows some improvement over that of *Leptomyrmea*, in that the oclusory tract is provided with somewhat sclerotized and therefore spring-like plicae, serving as adjuncts to the circular muscles in sealing the oclusory tract.

## TAPINOMA Förster

*Species examined: T. sessile\** (Say).

The proventriculus of *Tapinoma* (Fig. 26) is much more specialized in structure than any of the proventriculi discussed so far. It is a strong, rigid, subglobose structure, consisting of a well-developed bulb surmounted by a cupola made of thick, strongly sclerotized cuticle. The face of the cupola is ornamented with a characteristic, raised, densely pilose reticulum (Figs. 27, 28). This sculpturing extends inward to line the slit-like cruciform portal. This portal opens almost immediately into the bulb, and does not proceed farther inward to form an extensive occlusory tract as in *Leptomyrma* and *Liometopum*. The bulb itself is characterized by the extreme rigidity and c-shaped cross sections of the plicae (Figs. 26, 29).

The longitudinal musculature has undergone some new specialization (Figs. 27, 29). One group of fibers, consisting of only a few strands, joins the margins of the cupola to the sides of the bulb. On the basis of their position inside the circular muscles, I consider these fibers as homologues of *l.m.1* of previous proventriculi; from these they differ only in their more peripheral insertion on the cupola. A second group of longitudinal fibers inserts anteriorly on the crop intima, in such a way as to maintain the posterior fold surrounding the proventriculus, and originates posteriorly on the base of the bulb near the origin of the stomodaeal valve. This was the first proventriculus studied in which the full course of these fibers, including origin and insertion, could be traced with ease. Possibly they are homologues of *l.m.3* that have shifted their insertion outward to the crop intima and have taken posterior origin secondarily on the bulb. This interpretation is reasonable, in view of the absence of any other obvious *l.m.3* homologues in *Tapinoma*. There exists, in fact, some evidence that in previously discussed proventriculi, the outermost components of *l.m.3* are in a similar wise already fold-maintaining fibers, but in these cases origin and insertion could usually not be made out, and the fibers seemed to extend from the crop over the proventriculus without attachment to the cuticle. In view of the uncertainty that remains concerning the identity of these fibers in *Tapinoma*, and

subsequent dolichoderines having similarly placed fibers, they are labelled as *l.m.3*(?).

In its function as a dam, *Tapinoma* shows significant improvement over previous proventriculi. In the resting proventriculus, the quadrants of the cupola are rigidly maintained in the adducted position and the portal orifice is held to a narrow slit by the spring-like reinforcement of the strongly sclerotized plicae. *Here is seen the first instance in which proventricular damming is probably accomplished without any muscular reinforcement whatsoever.*

The structural advances in the *Tapinoma* proventriculus are, of course, linked closely with functional changes in the pumping action. The restriction of the portal orifice to a narrow slit tends to handicap the ingress of fluid during bulbar intake, and it becomes necessary to widen the portal through a disengagement of the cupolar quadrants. *Tapinoma* lacks an effective oclusory tract, and only a minimal dislocation of the quadrants suffices for the ready access of fluid into the bulb. I believe, in fact, that a wide disengagement of the quadrants is not only unnecessary but impossible. The thickness and rigidity of the cupola and the full sclerotization of the bulbar plicae (these acting as spring antagonists to the quadrant retractor muscles (*l.m.1*)) speak for a very narrow range of mobility of the quadrants. The narrowness of this range is further demonstrated by the resistance to displacement of the portal when a glass needle is inserted. It is interesting to note in this connection that *l.m.1* inserts on the rim of each quadrant, thereby achieving optimal leverage.

When the circular muscles contract, the bulb is compressed and fluid is forced back into the midgut in the usual fashion. Backflow into the crop is prevented by a maximal compression of the cruciform portal and a tight engagement of its pilose lining. During the subsequent relaxation of the circular muscles, the bulb expands under the intrinsic elasticity of its cuticular framework. In this expansion, the spring-like plicae play an important role. Simultaneously, the portal orifice is forced slightly agape under tension from *l.m.1*, and crop fluid rushes into the newly emptied and now expanding bulb.

## AZTECA Forel

*Species examined:* *A. sp.*\* (common ochraceous species from Vera Cruz, Mexico), *A. instabilis* (F. Smith).

Although in general shape, constitution of the bulb and arrangement of the musculature, the proventriculus of *Azteca* (Fig. 30) seems close to that of *Tapinoma*, it has certain features that suggest that it may stand alone as an evolutionary offshoot.

The cupola is unique in that the four quadrants are each deeply and angularly excised, lending the cupola a characteristic cruciform shape in frontal view. In section, the strongly sclerotized cuticle of the cupola is seen to possess an inner zone composed of closely approximated cuticular hairs which give it a finely and evenly striated appearance. These hairs extend inward along the cruciform portal to line a short oclusory tract. In possessing this tract, *Azteca* further differs from *Tapinoma*.

In musculature (Fig. 31) the *Azteca* proventriculus does not differ greatly from that of *Tapinoma*. Emery (1888) claimed a complete absence of longitudinal muscles in *Azteca instabilis* (F. Smith), but he probably just missed them.

The *Azteca* proventriculus at rest is maintained in the occluded state by its intrinsic elasticity in much the same way as in *Tapinoma*, and it can therefore also serve effectively as a passive dam to the crop. Its damming action is, in fact, improved over that of *Tapinoma*, owing to the presence of the oclusory tract.

Although obvious structural similarities render it likely that the proventriculus of *Tapinoma* and *Azteca* function in much the same way, it is not clear to me whether, during the active intake phase of bulb operation in *Azteca*, there is a full disengagement of the cupolar quadrants, or whether disengagement is damped as in *Tapinoma*. In *Azteca*, the presence of an oclusory tract may offer sufficient resistance to the inflow of fluids to make its opening necessary. The angular excision of each quadrant may confer greater flexibility upon the cupolar portal arrangement, thus facilitating the action of the strong "retractors" (*l.m.1*) found in *Azteca*. Further evidence for mobility of the oclusory tract is demonstrated by its relatively easy displacement when a glass needle is introduced.

The five genera *Forelius*, *Dorymyrmex*, *Turneria*, *Froggattella*, and *Iridomyrmex* are unmistakably related on the basis of

proventricular structure. In this series, the proventriculus achieves its highest degree of specialization among the Dolicho-derinae. An understanding of the structural intricacies of these proventriculi is perhaps best accomplished by considering first the most complex proventriculi of the series (*Iridomyrmex*, *Froggattella*, *Turneria*) and then their more simple evolutionary relatives (*Dorymyrmex*, *Forelius*).

### IRIDOMYRMEX Mayr

*Species examined:* *I. detectus*\* (F. Smith), *I. viridiaeneus*\* Viehmeyer, *I. punctatissimus* Emery, *I. nitidus* Mayr.

The proventriculus of *Iridomyrmex* (Figs. 32, 44, 45) features a broad, strongly reflexed cupola with involuted margins, holding tightly within its hollow a greatly reduced bulb. (Caste dimorphism is displayed in the relative development of cupola and bulb; in the female caste, the bulb is slightly larger, and barely projects from beneath the cupolar shell.)

The cupola is primarily divided into four quadrants by the cruciform portal in the usual fashion. A major new development is the secondary division of the quadrants, each of which is split radially by a narrow *phragma* (*phr.*).

The external cupolar cuticle is covered by dense, fine, short pile (Figs. 34, 35), extending into the cruciform portal. A similar pilose vestiture, but slightly longer, was already seen to cover the cupola of *Azteca*.

Each arm of the cruciform portal opens into a vestibular cleft or *sinus* (Figs. 32, 35; *sin.*), which in turn communicates with the mesial lumen of the bulb via a submedian zone of constriction (Figs. 32, 35; *a*). The zones of constriction are secondary developments within the bulb proper that have arisen in response to a functional need to be discussed below. The bulb is further characterized by the subdeltoid cross section of the plicae.

Histologically, the proventriculus is seen to lack all intrinsic longitudinal muscles (Figs. 34, 35). There remain only those fibers (*l.m.3*) that maintain the posterior fold of the crop surrounding the cupola.

An outstanding advance in *Iridomyrmex* is the complete encasement of the bulb within the rigid, reflexed cupola, a circumstance that tends to render the bulb motionbound. This handicap

has been overcome by the development of the cupolar phragmata, which act as flexible radial hinge-lines, allowing the cupolar segments to yield inward to the contraction of the bulb. The powerful development of the circular muscles (Figs. 34, 35) reflects the added burden imposed on the bulb by the need for embowing the cupolar segments during bulbar contraction. The bulbar expansion that follows is activated not only by the intrinsic elasticity of the bulb itself, but also by the cupolar segments, which, after becoming embowed during bulbar contraction, spring back to their original position and carry along the walls of the bulb.

The necessary development of radial hinge-lines, however, brings with it a new difficulty. During bulbar contraction, the lateral arms of the cruciform portal tend to be forced open by the contraction of the circular muscles (see Fig. 35) instead of becoming occluded, as would be the case if the cupolar quadrants were not pleated. It therefore has become necessary to develop a secondary valve seal in the form of the constriction zones within the bulbar lumen. During bulb contraction, the four constriction zones close early in each pumping cycle, and serve to prevent leakage from bulb to crop.

Since *Iridomyrmex* has lost all intrinsic longitudinal muscles, it is incapable of actively expanding the cruciform portal during bulb expansion. The need for such expansion is avoided by the reduction of bulb size (relative to portal orifice) and also because resistance to inflow is minimized in the absence of an occlusory tract.

This proventriculus is ideally suited to serve as a passive dam. The very narrow, densely pilose portal, maintained immobile by the rigid bracing of the bulbar core within the cupola, acts as an effective plug guarding the outlet of the crop; fluid can probably be forced inward past the portal only under suction pressure exerted by the bulb.

#### FROGGATELLA Forel

*Species examined: F. kirbyi* (Lowne).



## TURNERIA Forel

*Species examined: T. sp.\** (near *pacifica* Mann, collected by E. O. Wilson in New Hebrides, 1954-1955).

In these two genera the proventriculus is identical in all respects to that of *Iridomyrmex*. Caste dimorphism is again manifested in the slightly longer bulb in the female.

## DORYMYRMEY Mayr

*Species examined: D. ensifer\** Forel.

On the basis of the proventriculus, *Dorymyrmex* (Figs. 42, 43) may be considered close to the direct evolutionary antecedent of *Iridomyrmex*.

In *Dorymyrmex*, unlike *Iridomyrmex*, the posterior third of the bulb, constituting the most voluminous and therefore the contractile portion of the bulb proper, is free and projects from beneath the cupolar shell. Each cupolar quadrant is, as in *Iridomyrmex*, incised by radial hinges or phragmata, but incision is incomplete and stops considerably short of the cupolar summit. As in *Iridomyrmex*, the cupola and portal bear short dense pile, and the plicae of the bulb are subdeltoid in cross section. There is no trace of intrinsic longitudinal muscles, and there persist only those fibers (*l.m.3*) that sustain the circumcupolar fold of the crop (Fig. 37, representing a longitudinal section through the proventriculus of *Conomyrma*, may be taken also to represent *Dorymyrmex*). *Dorymyrmex* has not acquired the secondary valve-seal mechanism provided in the bulb of *Iridomyrmex* in the form of submesial zones of constriction.

From a functional standpoint, one can readily explain the incipient condition of quadrant incision, and the lack of a secondary valve-seal mechanism in the bulb. Both of these conditions are, in fact, directly attributable to the incompleteness of the envelopment of bulb by cupola. First of all, the fact that most of the contractile portion of the bulb projects from beneath the cupola, thereby remaining largely unimpeded in its operation, obviates the need for a complete radial incision of the quadrants. Only the rim of the cupola must yield to bulbar contraction, and consequently only the rim is incised. Secondly, since the quadrants are only incompletely pleated, it is still

possible to accomplish a valve-seal at the level of the portal during bulbar compression, and no secondary valvular mechanism had to be acquired.

In its action as a passive dam, the *Dorymyrmex* proventriculus presents the same structural advantages as that of *Iridomyrmex*.

### FORELIUS Emery

*Species examined: F. foetidus\** (Buckley).

In its basic plan, the proventriculus of *Forelius* (Figs. 40, 41) is just about what would be expected of a precursor member of the *Dorymyrmex-Iridomyrmex* line. *Forelius* displays in incipient form the outstanding feature of this line, namely the envelopment of the bulb by the cupola; most of the bulb is free, and only the anterior third is encased within the cupola. Relative to the cupola, the bulb is much larger in *Forelius*, than it is in *Dorymyrmex* and *Iridomyrmex*. *Forelius*, like *Dorymyrmex*, shows a beginning of eupolar pleating: only the margins of each quadrant are interrupted by phragmata. The subdeltoid outline of the plical cross section and the short dense evenly-distributed pile of the eupolar face and portal, characteristic of both *Dorymyrmex* and *Iridomyrmex*, are already fully developed in *Forelius*.

Histologically, the picture presented by the longitudinal muscles is puzzling (Fig. 36). The most conspicuous fibers (*l.m.?*) insert on the underside of the quadrants *outside* the circular muscles, bend posteriorly around the circumcupolar fold of the crop, and fan out anteriorly over the crop. These fibers would seem to represent a newly captured component of the proventricular musculature, possibly representing crop fibers that have secondarily inserted on the cupola. A single fiber (see ?, Fig. 36) is shown as a remnant of *l.m.1*. A question mark has been used to denote this fiber, since its presence is not of general occurrence, and I have, in fact, seen it only as a single fiber in one of the three proventriculi sectioned longitudinally (all were workers of the same nest series). This variation in the presence of *l.m.1* points to *Forelius* as an evolutionary stage in the *Dorymyrmex-Iridomyrmex* line at which *l.m.1* has become totally superfluous and is disappearing. Longitudinal fibers,

similar in position to *l.m.3* of previous proventriculi are present in *Forelius*.

Although its general structural affinities to *Dorymyrmex* suggest that the *Forelius* proventriculus functions in much the same way, there remains to be found a fully satisfactory explanation of the function of the unique longitudinal muscles (*l.m.?*) of *Forelius*. In view of their insertion on the underside of the quadrants, their obvious function would appear to be quadrant disengagement and portal widening. The general rigidity of the cupola (evidenced again in this genus by resistance to displacement when a glass needle is inserted through the portal) would, of course, preclude anything but the narrowest margin of eupolar mobility, and the most that the muscles can accomplish is a minimal distention of the portal slits (in much the same way as in *Tapinoma*). But why has portal distention become a necessity in *Forelius* when it is obviously superfluous in the basically similar proventriculi of *Dorymyrmex* and *Iridomyrmex*? The answer lies in the relatively larger size of the *Forelius* bulb, the undistended portal of which offers an insufficient intake orifice during bulbar expansion. One may ask why *Forelius* did not retain a fully developed set of *l.m.1* to accomplish portal distention instead of acquiring a completely new set of muscles, but careful examination of Figure 36 shows that *l.m.1*, due to its adaxial position, would be ill-suited to accomplish quadrant retraction even if strongly developed.

The following two genera (*Conomyrma* and *Technomyrmex*) have much in common with the *Forelius-Dorymyrmex-Iridomyrmex* line, but certain unique characteristics of their own suggest their phyletic divergence from this series.

### CONOMYRMA Forel

*Species examined: C. thoracica\** Santschi

*Conomyrma*, in common with *Forelius*, *Dorymyrmex* and *Iridomyrmex*, shows a partial envelopment of the bulb by the cupola, the degree of involvement being intermediate between that of *Forelius* and *Dorymyrmex* (Figs. 33, 46, 47). The eupolar cuticle bears short dense pile, and the bulbar plicae are sub-deltoid in cross section (Figs. 37, 38, 39). *L.m.1* fibers are totally lacking, and there are present only those longitudinal

fibers (*l.m.3?*) that maintain the circumcupolar fold of the crop.

*Conomyrma* differs from the *Forelius-Dorymyrmex-Iridomyrmex* series in that it has no phragmata to interrupt the strongly convex, evenly sclerotized surfaces of the quadrants. The four convex quadrants, separated by the recessed lines at the arms of the portal, produce a four-lobed or somewhat clover-leafed pattern in frontal view (Fig. 47).

The "yielding lines" in the cupola, needed to allow bulbar contraction, coincide with the arms of the cruciform portal. The elastic arch formed by each quadrant confers the necessary flexibility to allow recession at the "yielding lines" during bulbar contraction. The placement of the "yielding lines" at the portal slits also ensures a tight closure of the latter during contraction of the bulb, and this closure acts as an efficient valve opposing backflow. Thus, by means of a relatively simple variation in the cupolar plan, the *Conomyrma* proventriculus has avoided the development of phragmata and the ensuing difficulties that had to be met with in *Iridomyrmex* by the acquisition of a secondary valve-seal in the bulb.

#### TECHNOMYRMEX Mayr

*Species examined:* *T. detorqueus*\* (Walker) (= *albipes* F. Smith).

This proventriculus (Figs. 48, 49) is so similar to that of *Conomyrma* in the major features of its framework that one is bound to assume that it functions in identical fashion.

*Technomyrmex*, like *Conomyrma*, has acquired arched quadrants as a means of conveying flexibility to the cupola; the arching is more pronounced than in *Conomyrma* and affords a distinguishing character.

Emery (1888) and Forel (1878) have already pointed to the unique sculpturing manifested by the *Technomyrmex* cupola. In *T. detorqueus* this sculpturing takes the form of a reticulum of hexagonal units (Fig. 49), raised on the *underside* of the cupola. My preparations suggest (although not with certainty) that the hexagonal units delimit the areas of cuticular deposition of the individual underlying epithelial cells. Emery interprets the reticulum, not as a surface sculpturing, but as an intracuticular labyrinth; it is likely that he was led to an erroneous

interpretation by the obliquity of his sections.

*Technomyrmex* differs from *Conomyrma*, *Forelius*, *Dorymyrmex*, and *Iridomyrmex* in that the bulbar plicae are not subdeltoïd, but C-shaped in cross section (Fig. 49). This feature, the unique type of cupolar sculpturing, and also divergent external characters of the whole ant that have long been recognized by taxonomists (Brown, W. L., personal communication) point up the possibility that the form and function of the *Technomyrmex* proventriculus may have developed along an independent line. In this case, the proventriculi of *Technomyrmex* and *Conomyrma* would have to be counted as a striking instance of convergent evolution.

### Subfamily FORMICINAE

Among the formicine genera, the proventriculus falls far short of developing the heterogeneity of types we have seen to occur in the Dolichoderinae. In fact, all Formicinae possess either one or the other of two basic types of proventriculi, with relatively slight variation, except for the very few known species, belonging to only one or two genera, in which the proventriculus is of intermediate character. The two main types, with the intermediates, seem to express a simple evolutionary progression from the more generalized *asepalous* type to the advanced *sepalous* type. From among many possible examples, the two described here in detail as representative of *asepalous* (*Notoncus*) and *sepalous* (*Camponotus*) types were chosen because of their relatively large size and because adequately preserved material happened to be available.

#### Asepalous Formicine Proventriculus

##### NOTONCUS Emery

*Species examined: N. ectatommoides\** (Forel).

The cuticular framework (Fig. 50) consists of cupola and bulb, both characterized by extreme sclerotization and rigidity.

The cupola, unlike that of any dolichoderine proventriculus, is not hollowed out, but consists of a thick solid cuticular cap roofing the frontal aspect of the bulb. The face of the cupola is

flattened in *Notoncus* (but domed in many other asepalous formicine genera) and frames a narrow cruciform portal. The portal continues inward through the cupola in the form of a narrow oclusory tract, except for the outer extremities of the arms of the portal, each of which is immediately adjacent to the upper extension of its respective plicary canal (Figs. 53, 55-58). The face of the cupola, the cruciform portal, and the oclusory tract all bear short, densely approximated pile, similar to but longer than that found in the advanced dolichoderine proventriculi. The cruciform portal and oclusory tract are rigidly braced by the massive cupolar quadrants; it is impossible to pry open the portal with a glass needle without cracking the bulbar framework.

The bulb itself is marked externally by the four prominent plicae, one at each corner. The plicae are heavily sclerotized and c-shaped in cross section, so that the lumen of each one forms a distinct *plicary canal* (*pl. cn.*). Posteriorly, the bulb merges into the stomodaeal valve in much the same way as in all other proventriculi, by a posterior constriction and sudden thinning of the cuticle.

The proventriculus of *Notoncus*, like that of probably all the other asepalous formicine genera, is peculiar in that it does not intrude into the crop in dolichoderine fashion, but is actually prevented from such intrusion by a constriction of the crop immediately in front of the cupola (*precupolar constriction*: Figs. 53, 54, *precp. const.*).

Histologically, *Notoncus* has undergone some striking innovations (Figs. 53, 55-58). The circular muscles are most strongly developed around the bulb, and at this level they do not differ significantly in their arrangement from those of previously discussed proventriculi: the innermost fibers insert along the plicae, while the peripheral fibers envelop the bulb without cuticular attachments. Anteriorly, the circular muscles extend past the cupola to form a relatively strong sphincter surrounding the precupolar constriction of the crop. In this arrangement the *Notoncus* proventriculus differs from all previously discussed proventriculi, in which, it will be recalled, the strongly developed circular musculature terminates abruptly at the anterior extremity of the bulb, whence it continues as a loose network of fibers over the crop.

The principal group of longitudinal muscles (Fig. 53) I consider, on the basis of their position inside the circular muscles, as homologues of *l.m.1* of previous proventriculi. These fibers originate on the interplicary cuticle of the bulb and extend anteriorly to insert, *not on the cupolar quadrants*, as in previous proventriculi, but on the crop intima of the precupolar constriction, in such a way as to act as antagonists to the sphincter surrounding the constriction (some fibers apparently fail to insert on the cuticle and extend anteriorly over the crop; see Fig. 53).

Outside the circular muscles there is present, as usual, a second rather weakly developed group of longitudinal fibers. I am tentatively homologizing these with *l.m.3* of previous proventriculi, although their anterior insertion on the crop intima could not be verified with certainty in *Notoncus*.

Thus we see that the most important modifications of the musculature of the asepalous formicine proventriculus are correlated, on the one hand, with the loss of portal mobility, and on the other with the acquisition of the precupolar constriction. The development of a rigid immobile portal eliminated the need for longitudinal muscles of the kind needed for quadrant disengagement. The muscles were not lost, however, as occurred in the higher dolichoderines with similarly immobile portals; a shift of their anterior insertion engaged them instead with the operation of the precupolar constriction of the crop.

In its function as a dam, the asepalous formicine proventriculus presents the same advantages as that of the higher dolichoderines, inasmuch as the portal orifice is permanently reduced to a narrow, immobile and densely pilose slit, rigidly braced by the sclerotized cupola and plicae. Its damming function is actually improved over that of the advanced dolichoderine proventriculus by the presence of the oclusory tract.

It is in the pumping action of the proventriculus, and specifically in the mechanics of ingress past the cruciform portal and oclusory tract, that we find in *Notoncus* a functional deviation from previous proventriculi.

It will be recalled that almost the entire oclusory tract is by-passed at its four corners by an anterior extension of the plicary canals. These four tips apparently constitute the principal incurrent pathways, since they represent the points of least resistance to inflow. In conformity with this functional plan,

the oclusory tract is densely pilose, while the canals have naked walls. In this method of ingress, the *Notoncus* proventriculus differs from the dolichoderine proventriculi with similarly immobile portals. In these, there are no structurally differentiated pathways of resistance through the portal; resistance to inflow, and therefore rate of inflow, is generally distributed over the entire portal.

Following is my interpretation of the pumping action of the proventriculus. As the bulb cavity collapses under muscle contraction, the contents are forced back through the cylinder into the midgut. The entire oclusory tract becomes maximally occluded through a tight engagement of its pilose lining, and thus acts to bar backflow into the crop. Also, as the bulb starts its contraction, its four plicary canals are sealed off by approximation of their inner edges, perhaps imperfectly in the posterior portion, but at least completely enough to act as an auxiliary valve to prevent most of its contents from flowing back and forcing their way through the portal tips.

As the circular muscles relax and the bulb cavity expands due to the elasticity of its cuticular framework, the original narrow orifice of the cruciform portal is restored. Simultaneously the plicary canals open again into the bulb lumen and communicate the bulbar suction to the tips of the portal. Undoubtedly, some liquid is sucked in also through the oclusory tract, but this portion is so extensive and densely covered with hairs that traffic through it must be minor as compared to that through the lateral canal system.

What is the function of the precupolar constriction? If we follow the basic assumption that the longitudinal muscles contract alternately with the circular muscles, it is apparent that the constriction opens and the cupola is uncovered to project freely into the crop just at the time when bulb expansion has initiated fluid inflow through the portal. Thus, the opening of the constriction acts as a pump in itself, inasmuch as it assures the transfer of crop fluid to the immediately antecupolar lumen of the crop, and this function is probably especially important when the crop contains only small amounts of fluid. An additional function of the precupolar constriction is suggested below, on page 480.



## MELOPHORUS Lubbock

*Species examined*: *M. sp.*\* probably *ludius* Forel), *M. bagoti* Lubbock.

The outstanding peculiarity of *Melophorus* is to be found in the cupola (Fig. 52), the face of which is slightly depressed in the center and protuberant at its four corners. Otherwise, both in its cuticular framework and arrangement of the muscles (Figs. 59-61), the proventriculus does not differ grossly from *Notoncus*.

## ACROPYGA Roger

*Species examined*: *A. myops*\* Forel (or species near, collected by W. L. Brown, Blackall Range, S. E. Queensland, Australia, 1951).

## ANOPOLEPIS Santschi

*Species examined*: *A. longipes* (Jerdon), *A. custodiens* (F. Smith).

## ACANTHOLEPIS Mayr

*Species examined*: *A. frauenfeldi* (Mayr).

## DIODONTOLEPIS Wheeler

*Species examined*: *D. hickmani* (Clark).

The proventriculi of these genera (Figs. 51, 64, 65) resemble one another on the basis of the strongly convex shape of the cupola. *Diodontolepis*, which has not been illustrated herein, bears very close resemblance to *Anoplolepis*. Histologically, only *Acropyga* (Figs. 62, 63) was examined, and except for minor structural peculiarities, such as the extreme thickness of the plical walls, there were found no specializations in the arrangement of the muscularis to suggest a functional deviation from *Notoncus*. All these genera have a precupolar constriction like *Notoncus*.

## MYRMOTERAS Forel

*Species examined*: *M. williamsi* Wheeler.

The single dried specimen that was available of this rare

species revealed a distinctly peculiar proventriculus (Fig. 66), unique among those of asepalous formicine in the flattened and cruciform aspect of the cupola, and in the elongate and posteriorly tapering shape of the bulb. (Histologically preserved specimens of this genus have recently been collected by Dr. E. O. Wilson and should be available shortly to amplify the present study.)

#### Sepalous Formicine Proventriculus

(Figure 67, a diagrammatic representation of the sepalous proventriculus, should be used as a reference throughout this section.)

#### CAMPONOTUS Mayr

*Species examined:* *C. vicinus*\* Mayr, *C. americanus*\* Mayr, *C. herculeanus* (Linnaeus).

In the camponotine proventriculus (Figs. 67, 68, 70-74), the obvious distinctive character, here met for the first time, is a long anterior extension called the *calyx*, consisting of four heavily sclerotized strap-like cuticular arms, or *sepals* (*sep.*), extending anteriorly from the bulb to capture part of the posterior wall of the crop. (Sexual dimorphism is manifested in all sepalous proventriculi by the slightly longer calyx in the female.)

The sepals may be thought of as the anterior drawn-out bulbar plicae of an asepalous precursor, that have carried along in their extension the four corners of the cupola with their enclosed portal tips. Each sepal is seen to contain a cylindrical canal, the *sepal canal* (*sep. cn.*) (continuous posteriorly with the plicary canal of the bulb), that communicates along its entire length with the lumen of the calyx through a narrow and densely pilose longitudinal cleft (*pt.*) representing an extended arm of the cruciform portal. On their luminal surface, the sepals are covered with dense short pile (Fig. 71) similar to that lining the cupolar face of asepalous formicine proventriculi. The sepals themselves are joined by means of membranous sheets of *intersepalary cuticle* (*intersep.*), continuous with and of the same texture as the intima of the crop wall proper.

Posteriorly, the sepals curve together and fuse medially at the level of the oclusory tract. In the structure of the oclusory tract and bulb, *Camponotus* does not differ grossly from asepalous proventriculi, and the rigid c-shaped plicae are again so constituted that the canals they enclose merge with the bulb lumen by way of a zone of constriction that can be sealed off during bulb compression (Fig. 74).

Only relatively minor changes have occurred in the muscularis (Figs. 70-74). The *l.m.1* fibers are seen to originate on the interpleiary cuticle of the bulb, and extend anteriorly past the oclusory tract, at which point the inner fibers become inserted on the intersepalary cuticle, while the few remaining outer fibers continue anteriorly without cuticular attachments past the calyx and over the crop. Attention is called to the inward fold of the intersepalary cuticle at the bottom of the calyx (Fig. 70, *a*), and into which insert the *l.m.1* fibers. This fold is undoubtedly all that remains in this proventriculus of the preepupolar constriction of an asepalous ancestor.

Outside the circular muscles, a few scattered longitudinal fibers extend from crop to midgut (Fig. 70, *?*), apparently bypassing the proventriculus without cuticular attachments. Probably these fibers contain only the usual crop-to-midgut fibers, although it is possible that they are joined by homologues of *l.m.3* of previous proventriculi, that have here become detached from the cuticle. In other sepalous formicine genera (see *Formica* next below) the muscles differ in their arrangement.

In its action as a pump, this proventriculus remains essentially the same as its asepalous antecedent. The principal difference between the two types lies, of course, in the sepalary development and its functional consequences. In asepalous formicine proventriculi, the presence of an oclusory tract—although a distinct asset to the function of the proventriculus as a dam—considerably restricts the portal area available for bulbar intake. Only the outermost tips of the portal, being immediately adjacent to the anterior extensions of the four plicary canals that by-pass the oclusory tract, remain as pathways for fluid ingress. *Camponotus* and the other sepalous formicines have successfully exploited a means of increasing the bulbar intake area by extending, in the form of the calyx, both the plicary canals and their associated portal tips. Thus, the calyx is to be regarded, not as

an adjunct to the damming function of the proventriculus, but as a further refinement of the proventriculus as a pump. The damming potential has, however, been retained, since increase in portal area is accomplished without *widening* the portal at any point.

During bulb contraction, when fluid is being evacuated from the bulb through the stomodaeal valve, backflow through the oclusory tract is prevented by the tight engagement of its opposing pilose linings. Simultaneously, the potential backflow route through the plicary and sepalary canals is closed (or nearly closed) by the meeting of the edges of the grooves through which canals and bulbar lumen communicate. When the bulb recovers by means of elastic expansion, the grooves are reopened, and the lumen again communicates with the canals, initiating a new inflow through the sepalary portal slits. As in the asepalous formicines, it seems that a small amount of fluid must also enter directly through the oclusory tract at the stage of expansion; however, the length, narrowness, dense vestiture and extremely restricted mobility of the four clefts forming the tract surely reduce such inflow to a negligible quantity, especially when one considers the opportunity for fluid ingress offered by the portal-plus-canals.

Emery (1888) believed the calyx to function exclusively as a valve that, by sustained occlusion, acts to relieve the proventriculus of fluid pressure from the crop. He disregarded the possibility that the principal intake system of the bulb might be routed through the sepals. He believed that the pilose lining of the portal clefts actually seals off the sepal canals from the calyx cavity: "Die Rinne wird gegen das Lumen des Kelches durch das Ineinandergreifen der die Flügel besetzenden Härchen verschlossen." Accordingly, he was inclined to treat the sepals as relatively unimportant structures. Subsequent workers, including Forbes ('38), have observed that the canals really open into the lumen, but not until recently (Eisner and Wilson '52) has the possibility been considered that they might serve to conduct fluid past the oclusory tract.

Brief mention should be made at this point of an incidental, but probably significant function of the calyx. It is likely that during bulbar activity the calyx undergoes pulsations synchronous with those of the bulb, being alternately constricted by its

circular muscles and expanded by the elastic spring-like action of the sepals. During calyx expansion, crop fluid tends to be drawn into the calyx lumen, thereby assuring an adequate supply of the bulb just at the time when bulb expansion initiates fluid intake through the sepal-portal arrangement. Thus, while increase of intake area was the principal evolutionary justification for the appearance of the calyx, it seems that it came to function also as an analogue of the precupolar constriction of asepalous proventriculi.

It is doubtful that the *l.m.1* fibers play any significant contributory role in the expansion of the calyx, since they insert, not on the sepals themselves, but on the loosely folded and flaccid intersepalary cuticle. Furthermore, in other sepalous formicines (*Formica*), the similar structure of which suggests no great functional divergence from *Camponotus*, *l.m.1* has been lost entirely. I regard *l.m.1* in *Camponotus* as a mere remnant persisting from an asepalous antecedent in which the function of *l.m.1* was, as in *Notoncus*, the dilation of the precupolar constriction.

### FORMICA Linnaeus

*Species examined*: *F.* sp.\* (*fusca* group), *F. subnuda* Emery (*sanguinea* group).

Aside from obvious but relatively minor differences in the shape of the bulb and calyx, *Formica* (Figs. 69, 75, 100-103) differs significantly from *Camponotus* only in the arrangement of the longitudinal muscles (compare Figs. 70 and 75). *l.m.1* is entirely absent. There is present, outside the circular muscles, a group of longitudinal fibers that insert anteriorly on the crop intima so as to maintain a circumsepalary fold of the crop (Fig. 75); I am tentatively homologizing these fibers with *l.m.3* of previous proventriculi. In *Camponotus* (Fig. 70) no such circumsepalary fold was found, and the scanty outermost longitudinal muscles of the proventriculus extend from crop to midgut without apparent cuticular connections.

Figures 76-84 illustrate a variety of the forms of cuticular framework found among different sepalous formicine genera, included here chiefly because of their taxonomic interest. The features of each type as known at this time are clear from the

figures, and the individual cases require no discussion. (In *Myrmecocystus* (Fig. 79) the tips of the sepals curve outward only in the worker; in the female they are straight.)

Proventriculi were examined for a number of additional genera, but since each of these closely resembles one of the genera figured, it will suffice here merely to list the correspondences. *Gigantiops destructor* (Fabricius), *Dendromyrmex chartifex* (F. Smith), *Opisthopsis haddoni* Emery, and *Polyergus breviceps* Emery resemble *Formica*. *Polyrachis dives* (F. Smith) is similar to *Camponotus*. *Pseudolasius mayri* Emery closely resembles *Lasius*.

Although such characters as the shape of bulb and plicae and length of the sepals may in themselves be valuable phyletic indicators, it is hoped that the internal evolutionary relationships of this series will be further clarified by future work, and especially by a comparative histological analysis of the longitudinal musculature. The possibility should not be lightly dismissed that a major phylogenetic divergence may be outlined by the presence or absence of *l.m.1*, as exemplified in this study by *Camponotus* and *Formica* respectively.

#### Proventriculi with Incipient Sepals

##### CLADOMYRMA Wheeler

*Species examined: C. hewitti* Wheeler.

Only two dried specimens, a queen and a worker, probably nestmates, were available for study of this very rare genus. The proventriculus of the queen (Fig. 85) shows an incipient but nevertheless distinctly typical calyx, and on this basis *Cladomyrma* would seem to represent a survivor of the ancestral stock that gave rise to the higher sepalous formicines. Sexual dimorphism is strikingly exemplified in this genus by the *complete absence of a calyx in the worker*, the proventriculus being endowed with a typical asepalous cupola.

##### MYRMECORHYNCHUS André

*Species examined: M. emeryi* André.\*

Although distinctly suggestive of an incipient sepalar condition (Fig. 86), other peculiarities of the proventriculus, as well

as characteristics of the whole ant (W. L. Brown, and E. O. Wilson, personal communication), point to the possibility that *Myrmecorhynchus* may stand apart as an evolutionary offshoot, having acquired its sepal-like structures by convergence.

The bulb is more capacious than usual (Fig. 89), and the oclusory tract is not reduced to a narrow impassable cleft as in other formicines, but is seen to be held agape (Fig. 88), suggesting that bulbar intake is generally distributed over the entire portal and oclusory tract instead of just at the tips. Most probably, this widening of the oclusory tract developed in response to the increase in bulbar capacity. The cruceiform portal also differs from other formicines in that it lacks the usual pilose vestiture.

In its musculature, *Myrmecorhynchus* is like *Notoncus*. The precupolar constriction and *l.m.1* are well developed and probably still functional.

## PONEROID COMPLEX

Only very few representatives of this complex, including one or two genera of each of the four major subfamilies currently recognized (Brown '54), were examined for the present study. In part this was due to the lack of properly preserved material, an especially unfortunate handicap here since the relative uniformity of the cuticular framework of the poneroid proventriculus forces one to turn to the arrangement of the muscles in the search for phyletic indicators. The aberrant subfamily Leptanilinae could not be studied at all; I did not succeed in recovering a proventriculus from the single dried specimen that was available to me.

### Subfamily PONERINAE

#### ODONTOMACHUS Latreille

*Species examined*: *O. haematoda*\* (Linnaeus), or near.

In its principal features (Fig. 90), the proventricular framework conforms to the general plan of *Myrmecia*. The bulb is elongate and posteriorly tapering. Only the interplinary plates are somewhat sclerotized; the plicae themselves are thin and flaccid. The cupolar quadrants are globose, and diverge from

one another, framing a widely gaping cruciform portal. The presence of *l.m.1* and *l.m.3*, similarly arranged as in *Myrmecia*, could be determined with certainty. The apparent absence of *l.m.2* is not to be taken as conclusive, since my preparations were inadequate.

Both in its pumping action and damming potential, the proventriculus of *Odontomachus* probably resembles that of *Myrmecia*.

### AMBLYOPONE Erichson

*Species examined: A. australis*\* Erichson.

This proventriculus (Fig. 91) is strikingly unique among those of ants, and possibly all other Hymenoptera, in that it deviates from the basic quadripartite plan. The cupolar quadrants, portal arms, plicae, and interpleurary plates are six in number, instead of the usual four. Except for this remarkable feature, *Amblyopone* does not differ greatly from *Odontomachus*. The cupolar quadrants are more closely approximated, and do not diverge apically as in *Odontomachus*. The plicae are membranous, and the entire proventriculus is weakly sclerotized and flaccid. The material available was poorly preserved, rendering impossible an exact delineation of the longitudinal musculature. The *l.m.1* fibers are grouped into six separate bundles instead of the usual four, each bundle following the course of its corresponding interpleurary plate.

The structural peculiarities of *Amblyopone* do not suggest any major functional deviations. Its function, like that of *Odontomachus*, is probably similar to that of *Myrmecia*.

*Amblyopone* is generally agreed to be one of the most primitive of all living ants. The distinct peculiarities of its proventriculus point up the possibility that *Amblyopone* may actually be more highly specialized than previously suspected.

### Subfamily CERAPACHYINAE

#### PHYRACACES Emery

*Species examined: P. dumbletoni* Wilson.

Although distinctive in its barrel-shaped bulb (Fig. 92), the



proventriculus of *Phyracaces* conforms to the structural plan of *Myrmecia*, and presumably functions in a similar way. The presence of *l.m.1* and *l.m.3*, arranged as in *Myrmecia*, was determined with certainty, but there remains some doubt about the apparent absence of *l.m.2*.

### Subfamily MYRMICINAE

#### POGONOMYRMEX Mayr

*Species examined*: *P. occidentalis*\* (Cresson).

The cuticular framework (Fig. 95) consists of an elongate, extremely flaccid and funnel-shaped "bulb," devoid of a cupola, merging anteriorly with the crop through a gradual expansion of its lumen. Although the wall of the bulb is produced into four inward folds, vaguely delimiting plicary and interplicary regions (Fig. 96), there are no textural differences between these regions, the cuticle being evenly membranous throughout. The circular muscles are strongly developed as usual, but have lost all cuticular connection. The exact course and homologies of the longitudinal muscles could not be determined. The principal group of fibers, extending as four bundles along the inward folds of the bulbar cuticle, are strongly suggestive of *l.m.1*.

It is difficult to explain the functional implications of the obviously degenerate condition of this proventriculus. The loss of an anterior valve-seal, elsewhere provided by the cupola, and the loosely-folded membranous condition of the bulbar cuticle, speak for a radical departure from the usual fluid pumping action. It may well be that this type of proventriculus has become modified to yield to the passage of solid matter, forced through the bulb under muscular pressure. This possibility deserves further attention, especially since the myrmicines are known for their unusual feeding habits, several genera commonly partaking of seeds and other vegetable material.

The structural divergences of the *Pogonomyrmex* proventriculus would not seem to have reduced its capacity as a dam, since the membranous bulb is readily oclusible under muscular contraction.

Forel (1878) and Emery (1888) called attention to the highly aberrant proventriculus of the myrmicine tribe Cephalotini. This proventriculus has re-acquired a cupola, in the form of a rigid

and elaborately ornamented umbrella, that abuts a typical funnel-shaped and membranous myrmecine "bulb." The functional significance of this unusual eupolar development is obscure at present.

### HYLOMYRMA Forel

*Species examined: H. columbica\** Forel, or near.

This proventriculus is identical in all major respects to *Pogonomyrma*.

### Subfamily DORYLINAE

#### ECITON Latreille

*Species examined: E. hamatum\** (Fabricius).

This proventriculus (Fig. 93), although closely resembling that of *Pogonomyrma*, appears to have progressed even further in its degeneration, the folding of the bulbar cuticle being completely randomized and irregular (Fig. 94). This proventriculus is, in fact, nothing but a stomodaeal valve, preceded by a muscularly maintained constriction of the posterior wall of the crop.

The same functional speculations advanced for *Pogonomyrma* apply to *Eciton*, except that the latter is wholly predaceous.

### THE STOMODAEAL VALVE

Except in *Myrmecia*, where it was described in considerable detail, no emphasis has been granted to the stomodaeal valve in the various other proventriculi. The valve is, in fact, the most uniform constituent of the ant proventriculus, and the only structural modifications that seem to have functional overtones occur in the degree of development of the muscular sphincter that surrounds the neck of the valve at the point where it pierces the midgut.

In *Myrmecia*, as well as in all other generalized proventriculi with divergent eupolar quadrants and a mobile portal (pseudomyrmecines, ponerines, and cerapachyines), the sphincter is strongly developed, and probably serves in maintaining an occlusion of the neck of the valve when the resting proventriculus prevails in its function as a dam. In all the higher dolichoderines

and formicines, in which proventricular damming is accomplished passively by an elastically maintained occlusion of the cupolar or sepalar portal arrangement, the need for sustained occlusion at the level of the stomodaeal valve has been lost, and the sphincter surrounding the neck of the valve has accordingly become reduced, sometimes consisting of not more than a single layer of fibers.

#### IDENTITY OF THE "SEKRETSCHICHT" OF EMERY (1888)

Emery granted some emphasis to the fact that the cupola of most dolichoderine proventriculi seen by him (*Tapinoma*, *Technomyrmex*, *Forelius*, *Conomyrma* (= *Dorymyrmex* Emery nec Mayr), *Bothriomyrmex* and *Iridomyrmex*) is tightly overlain by a discrete layer or "membrane" of varying thickness. Emery assumed that this layer, which he called in its different forms *Sekretschicht*, *Sekrethäutchen*, or *Sekretblättchen*, was a deposit secreted by the cupolar epithelium. He found no such layer present in *Azteca*, *Liometopum*, *Leptomyrmex*, or tribe Dolichoderini. Among the formicines, Emery found the layer present in *Camponotus ligniperdus*, but makes no mention of it in the two asepalous genera he examined, *Plagiolepis* and *Brachymyrmex*.

In the histological preparations made for this work, a dense layer, more or less unevenly granulose in texture (Fig. 98), was found covering the cupola or sepals of the following genera:

Dolichoderinae: *Forelius*, *Dorymyrmex*, *Iridomyrmex*, *Turneria*,  
*Conomyrma*, *Technomyrmex*.

Formicinae: *Camponotus*, *Formica*.

The layer varied considerably in thickness, even among nest-mates. Structurally, it showed considerable differentiation from genus to genus, particularly in texture and in staining reaction; in some cases the layer was weakly basophilic, in others totally refractory to the stains used.

There was no trace of a layer in *Myrmecia*, *Pseudomyrmex*, *Aneuretus*, *Tapinoma*, and members of the poneroid complex. In *Azteca*, *Liometopum*, and *Leptomyrmex*, as well as in all genera of asepalous Formicinae that were sectioned (*Notoncus*, *Melophorus*, and *Acropyga*), there was present no compact

layer, but the cupolar hairs held some clustered particles in loose irregular arrangement (Fig. 99).

It is evident that the degree of development of the layer is closely correlated with the amplitude of portal mobility. With the notable exception of asepalous formicines, a *compact* layer is present only in those proventriculi endowed with an immobile slit-like portal. Given this correlation, my interpretation of the "Sekretschiicht" is that it is most likely not a secreted structure, but merely a filtration aggregate consisting of those small particles that, having escaped the withholding action of the infra-buccal chamber and the filtration devices within the buccal cavity, have massed on the cupolar or sepalar surfaces, held back by the filtering guard hairs of the proventricular portal.

There remains to be explained the absence of the layer in the asepalous formicines. The precupolar constriction may afford this explanation, considering its probable action of sweeping the cupolar face repeatedly during the pumping cycle (see under *Notoncus*, p. 468).

One apparent inconsistency in this hypothesis is the difference found between *Tapinoma* and *Forclius*, despite the similar functions proposed for these genera insofar as their damped portal opening is concerned. *Tapinoma sessile* lacked the filtrate layer in my preparations, while my *Forclius* possessed the layer in a well-developed form. The probability that the portal does open would at first glance seem to render difficult the accumulation of sufficient filtrate to form a layer, but the degree to which this opening is damped in these two genera actually makes it more surprising that *Tapinoma* lacks the layer than it does that *Forclius* has it.

As noted above, Emery found the layer present in *Tapinoma*, but in a different group of the genus, in *T. melanocephalum* (Fabricius). Absence of the layer in my *Tapinoma* could be taken as a sign that my interpretation of proventricular function is incorrect, and that the portal really opens more widely than seems possible in view of the cupolar rigidity. However, the structural qualities of the *Tapinoma* proventriculus lead me to believe that the lack of a filtrate layer in my limited samples is either a histological artifact or else reflects a lack of particulate dietary constituents in these specimens, all drawn from a unidial series.

PART III  
DISCUSSION

One of the organs long used in ant classification is the proventriculus, a structure in which major changes are largely concordant with subfamily, and even with many tribal breaks based primarily on other structural characters. It is this concordance that renders proventricular structure such a valuable indicator of phylogeny within the ants, and at the same time affords a basis for checking evolutionary steps in proventricular modification. Even at the generic level, the proventriculus so far as known offers no serious contradiction to presently accepted classifications, and the deeper one probes into the details of musculature and other components, the more new useful information the organ yields for the systematist.

In Figure 97, a dendrogram is based on the structural relationships of the known proventriculi as revealed by the present study, and interpreted in the light of the most recent phyletic schemes. It will be necessary to refer to this figure in following the discussion below.

The outstanding feature of the adult hymenopterous digestive tract is the crop, a stomodaeal food reservoir acquired in adaptation to the relatively discontinuous feeding habits characteristic of these insects (Bischoff '27). The proventriculus is essentially a structure accessory to the crop, and in this capacity serves both as a *dam*, capable of containing the pressure exerted by the liquid crop contents, and as a *pump*, regulating the delivery of fluid to the midgut. It consists of a flexible but strongly-muscled bulb, the pump, with intake and exhaust valves provided respectively by the eupolar portal, and the stomodaeal valve. The stomodaeal valve is embraced by a sphincter, the sustained contraction of which presumably effects the dam.

This simple type of proventriculus is well suited to the habits of the solitary Hymenoptera, the crop of which stores food for its own use, or at the most for the use of itself and its mate (Given '54).

With the acquisition of social habits and division of labor, the burden of securing, transporting and transmitting food falls entirely upon a part of the adult population. The brood, re-

productives, and non-foraging workers are more or less continuous consumers of food, but contribute little or nothing to the larder. There thus arises a necessity for a storage system — a necessity accentuated under unfavorable environmental conditions. Honeybees, for instance, solve this storage problem by means of the comb, a communal storehouse external to their own bodies.

In the ants, such storage facilities as exist, at least for fluids, are usually limited to the crops of the individual workers. The storage of amounts of fluid far in excess of the needs of the individual worker, and for protracted periods of time, places a strain on the arrangements by which damming depends upon sustained muscular contraction of the stomodaeal valve sphincter. Any structural changes tending to relieve the load of the sphincter are therefore at a premium, especially if these changes can shift the load to a passive barrier.

#### The generalized formicid proventriculus

In the lower ants (Ponerinae, Cerapachyinae, Myrmeciinae, Pseudomyrmecinae, and Aneuretinae) the proventriculus is similar in all major respects to that of the other Hymenoptera so far studied. Proventricular damming is probably maintained exclusively by the stomodaeal valve sphincter, which in these ants is especially well produced. The bulb is a flaccid structure with gaping portal, incapable in itself of plugging the crop. Damming is therefore a dynamic, energy-consuming process. This basically inefficient mechanism limits the full exploitation of the social functions of crop storage and regurgitative feeding. Indeed, recent work emphasizes the fact that in these primitive ants, regurgitative feeding is still in its incipient stages (Le Masne '53, Haskins and Whelden '54). None of these ants is known to have "replete" castes.

#### Dolichoderinae and Formicinae

In the advanced dolichoderines (tribe Tapinomini) and all formicines, proventricular damming no longer depends upon the continuous muscular pressure of the stomodaeal valve sphincter, and the sphincter in these subfamilies is greatly reduced in size.

The damming function has shifted to the reinforced cupola, which now forms a rigid shield, pierced by a narrow, densely pilose cruciform slit, and capable by itself of stemming leakage from the crop. Damming is therefore accomplished passively, without expenditure of muscular energy. The evolution of the proventriculus in these subfamilies is the history of the elaborate and varied pathways of change along which the proventriculus adapted to its new function as a passive dam.

An early step in the evolution of the damming cupola is exemplified in the dolichoderines by the *Azteca-Tapinoma* proventricular type, and in the formicines by the *asepalous* type. Already these proventriculi have acquired the pilose portal slit, strongly braced by the sclerotized cupola and bulbar plicae, and able to hold back fluids when the inactive proventriculus prevails in its function as a dam. That these remarkably similar refinements arose convergently in the dolichoderines and formicines is attested by the differences in the arrangement of the longitudinal muscles and by other characters.

The restriction both in size of orifice and in mobility of the cupolar portal arrangement — although a distinct asset to the damming function of the proventriculus — tends to render the portal orifice inadequate for bulbar intake during the pumping cycle. This handicap is accentuated in *Azteca* and the asepalous Formicinae by the interposition, between portal and bulbar lumen, of an occlusory tract. In order to reconcile the basic pumping action of the bulb with the new damming qualities of the portal, *Azteca* and *Tapinoma* retain a limited range of portal mobility, the quadrants being slightly dislocated during bulbar intake under the action of *l.m.1* muscle fibers. Dislocation is damped, with the sclerotized bulbar plicae acting as spring antagonists to the retractor muscles. Unlike those of *Azteca* and *Tapinoma*, the asepalous formicine proventriculus can accomplish its pumping action without quadrant dislocation. It has, in fact, no muscles adapted to moving the quadrants, the *l.m.1* fibers having shifted their insertion away from the cupola itself to become concerned with the operation of the precupolar constriction of the crop. Bulbar intake is routed through the plicary canals, the anterior extensions of which by-pass the occlusory tract to join the four corners of the portal. This mechanism of ingress, although using only a relatively small portion of the

portal, must provide sufficient flow for the active pumping action of the organ.

The most advanced proventricular types of the dolichoderines (*Iridomyrmex*, *Dorymyrmex*, *Conomyrma*, and *Technomyrmex*) and formicines (*Camponotus*, and all other *sepalous* proventriculi), although differing radically in structure, are actually remarkably similar in their functional achievements. They retain the narrow slit-like portal attained by their respective evolutionary antecedents, and are therefore similarly adapted to serve as passive dams. In these proventriculi, the need for portal disengagement is completely eliminated, and the quadrant retractors (*l.m.1*) are entirely absent, or if retained, as is the case in some *sepalous* proventriculi (*Camponotus*), they are functionally impotent as retractors. The complete loss of portal mobility is coincident with certain structural refinements designed to increase the *portal orifice: bulbar capacity* ratio needed to assure adequate bulbar intake during the pumping cycle. In the dolichoderines this is accomplished by a reduction in bulbar capacity through progressive envelopment of bulb by cupola, a process shown in its incipient stage in *Forclius*, and culminating in *Iridomyrmex*. In the formicines, bulbar capacity remains unaltered, there being instead an increase in the portal orifice through anterior extension of the portal tips in the form of sepals. Since the portal is increased in *length* but not in *width*, its damming potential is not sacrificed. The development of sepals is seen in its incipiency in *Cladomyrma*.

Two relatively primitive dolichoderine genera, *Liometopum* and *Leptomyrma*, having in common certain proventricular specializations unique among the dolichoderines, apparently represent one or two isolated and probably long-standing evolutionary offshoots. Both proventriculi feature an extensive oclusory tract, a distinct asset to the damming action of the proventriculus. Potentially, this oclusory tract tends to obstruct bulbar operation, but since it is articulated laterally by membranous plicae, it is easily opened by *l.m.1* during bulbar intake.

The adaptive significance of the passive-dam proventriculus of the dolichoderines and formicines is reflected by the full exploitation in these ants of the social functions of crop storage and regurgitative feeding (Le Masne '53). All ant genera known



to have "replete" castes are restricted to one or the other of these subfamilies.

### Myrmicinae and Dorylinae

The proventriculus of the myrmicines (with the exception of the Cephalotini; see Emery 1888) and the dorylines has become degenerated to the point where it consists essentially of only a stomodaeal valve; the bulb is presumably non-functional as a pump, since it is reduced to a membranous and more or less irregularly folded constriction of the posterior crop. From the structure of the organ it is clear that proventricular damming is not a passive process, but must be dependent upon muscular contraction, at the level of the stomodaeal valve and/or the "bulb." Although regurgitative feeding is known to occur among some of these ants (*Crematogaster*; Wilson and Eisner '57) nothing is known about the length of time over which the crop can store nutrient. It is interesting to note in this connection that some myrmicines have become independent of the crop as the exclusive communal reservoir. Instead, they have developed a storage system outside their own bodies, hoarding seeds or other types of solid nutrient.

It may be relevant here to emphasize a major functional limitation of the passive-dam dolichoderine and formicine proventriculi. The complete loss of portal mobility, resulting from the acquisition of a rigid slit-like portal, would seem to preclude completely the transfer of any but the most minute particulate matter to the midgut. We have seen, in fact, that in the advanced dolichoderines, even minute particles are not always passed to the midgut, but actually accumulate over the cupolar face in more or less discrete layers. We have also seen that in the asepalous formicine proventriculi, such accumulation of particles does not take place, presumably being prevented by the sweeping action of the precupolar constriction of the crop.

It would be interesting to know whether, in all ants with a rigid slit-like portal, there has been an increasing dependence upon cephalic solid-withholding devices such as the infrabuccal chambers or the ridges of the buccal cavity mentioned by Wheeler ('10). It would even be worthwhile considering whether the refinement of such buccal particle-traps was a pre-

adaptation necessary for the evolution of the passive-dam proventriculus. There is much need for detailed observations on the feeding behavior of ants having such proventriculi. Just because an ant is seen feeding on a dead insect, for instance, does not mean that it is *swallowing* solid matter, since it may actually take in only the juices. One would even expect that small particles such as pollen grains, which are known to figure prominently as a source of protein in the diet of adult honeybees, are of too large diameter to be transferred through the passive-dam proventriculi.

The proventriculi with mobile portals, on the other hand, such as those of the myrmicines, pseudomyrmecines, aneuretines, ponerines, and cerapachyines (and, for that matter, of all other aculeate families in which the organ has been studied), are constructed in such a way that no hindrance would appear to be offered to the passage of at least small particles. Perhaps some lesser particles such as pollen grains actually constitute a staple source of protein in some of these ants. From the work of Bailey ('52) we know, for instance, that in *Vespa*, *Bombus*, and *Prosopeis*, pollen suspensions do not choke the proventriculus and are effectively pumped to the midgut. In *Apis*, the proventriculus has certain structural peculiarities enabling it, at least under some circumstances, to strain out the pollen grains from the fluid crop contents and selectively transfer them to the midgut (Bailey '52, Schreiner '52). This type of activity, while probably incidental to the primary fluid-handling function of the proventriculus, may be of importance when the bee requires large quantities of pollen protein for the synthesis of brood-food secretion (Bailey '54). Whether any activity similar to the pollen-transfer action of the *Apis* proventriculus occurs in any of the ant proventriculi with mobile portals remains to be shown.

The proventricular structure of the dorylines and myrmicines (with the single known exception of the cephalotines) presents no obvious obstacle to the passage of even large particles, but we do not yet know whether these ants actually *swallow* solids. It would be interesting to know this, because it is not beyond possibility that the "degenerate" condition of the proventriculus in these ants is actually an adaptive response to changed feeding habits involving greater use of injected solids.

I am fully cognizant of the fact that the often elaborate functional schemes advanced here for the various proventricular types are largely speculative, and that future work may uncover fallacies in my reasoning. However, there is only one basic assumption underlying this study and for which I have no direct substantiating evidence, namely, that the circular muscles and longitudinal muscles contract alternately rather than simultaneously. Actually, it seems impossible to conceive of any workable proventricular mechanism based on a synchronous activity of these muscles. The other lines of reasoning used in connection with functional interpretations, such as evaluation of the relative effectiveness of the various muscles, are not completely speculative, since they are based in part on an estimation of the relative mobility of the various proventricular components that these muscles operate. Mobility of the cupolar quadrants, for instance, is readily disclosed by prying with a glass needle. Similarly, the elasticity of the bulb can be evaluated by observing its resilience under varying pressure directly applied.

It would be interesting to test the functional schemes advanced here by direct experimentation. I have not yet tried to evaluate the relative damming efficiency of the various proventricular types by determining 1) the amount of fluid that can be stored in the crop, and 2) the length of time over which storage can be maintained. However, such studies, and others along these general lines, are currently planned or already under way in this laboratory. The use of radioactive tracers appears to be especially promising. A preliminary investigation on the relative importance of regurgitative feeding in several representative species of ants is in press (Wilson and Eisner '57, Eisner and Wilson, '57).

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## KEY TO ABBREVIATIONS

The measurements given for proventricular length were taken between cupolar summit, or sepal tips, to the base of the bulb at the point of insertion of the stomodaeal valve.

All longitudinal sections show only one half of the proventriculus, and are taken through the interplenary cuticle of the bulb, midway between the plicae.

<i>bl.</i> .....	bulb
<i>b.m.</i> .....	basement membrane
<i>c.m.</i> .....	circular muscles
<i>cp.</i> .....	cupola
<i>Cr.</i> .....	crop
<i>interpl.</i> .....	interplenary plate of bulb
<i>intersep.</i> .....	intersepalary cuticle
<i>l.m.1</i> .....	longitudinal muscles no. 1
<i>l.m.2</i> .....	longitudinal muscles no. 2
<i>l.m.3</i> .....	longitudinal muscles no. 3
<i>M. G.</i> .....	midgut

<i>occ. tr.</i> .....	occlusory tract
<i>phr.</i> .....	phragma
<i>pl.</i> .....	plica
<i>pl. cn.</i> .....	plicary canal
<i>precip. const.</i> .....	precipolar constriction
<i>pt.</i> .....	portal
<i>pv.</i> .....	proventriculus
<i>qd.</i> .....	quadrant
<i>sep.</i> .....	sepal
<i>sep. cn.</i> .....	sepal canal
<i>sin.</i> .....	sinus
<i>st. vlv.</i> .....	stomodaeal valve